HELIANTHUS LAETIFLORUS AND HELIANTHUS RIGIDUS — HYBRIDS OR SPECIES?

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The identification of perennial sunflowers has long been a persistent source of difficulty, resulting in a large part from the blurring of species lines by hybridization. Through field and experimental studies, it has been established that interspecific hybridization between diploid members of the genus is common (see Heiser *et al.*, 1962, for references). In the present paper four hexaploid taxa, *Helianthus laetiflorus* Pers., *H. rigidus* (Cass.) Desf., *H. subrhomboideus* Rydb. and *H. tuberosus* L. are considered.

Although *H. tuberosus* has been accepted as a species by all who have worked on the genus, the other three taxa have been treated in a variety of ways. Watson (1929) recognized *H. laetiflorus* and *H. rigidus* as distinct species and considered *H. subrhomboideus*, a synonym of the latter; he also described two new species, *H. suberbus* and *H. severus*, which we feel should be referred to *H. laetiflorus*. Fernald (1946) recognized but a single species, *H. laetiflorus* and treated *rigidus* and *subrhomboideus* as varieties. Cronquist (1952) accepts but a single species, *H. laetiflorus*, and recognizes no varieties.

We would like to extend thanks to the curators of the following herbaria: University of Arkansas, Duke University, Gray Herbarium, Michigan State University, Missouri Botanical Garden, New York Botanical Garden, University of Wisconsin, and the United States National Herbarium. The distributions shown in the maps have been compiled from the specimens in these herbaria and the ones at Indiana University. We would also like to thank Prof. J. Leandri of the Museum National d'Histoire Naturelle, Paris, who furnished us with the photograph of the type of *H. laetiflorus*. Type material of *H. subrhomboideus* in the herbarium of the New York Botanical Garden has also been examined, but we have not yet been able to secure authentic material of *H. rigidus* and our interpretation rests on Cas-

sini's original description. A grant to the senior author from the American Philosophical Society made it possible to examine certain European types. This research was also aided by a grant from the National Science Foundation to the junior author.

DISTRIBUTION: *Helianthus subrhomboideus* (Fig. 1) is a prairie plant widely distributed in Canada from Alberta east to Quebec and extending southward through the plains to western Texas and New Mexico. *Helianthus rigidus* (Fig. 2) is found in the central United States and in the northern and western portion of its range is sympatric with the preceding species. These two species may be found occasionally in the eastern United States as adventives or escapes from cultivation. The third taxon, *H. laetiflorus* (Fig. 3), has a scattered distribution in the central United States where it is usually associated with both *H. rigidus* and *H. tuberosus* and has a spotty distribution in the east, where it has been widely cultivated as a garden ornamental. Many plants of *H. laetiflorus* from the east are seed sterile probably indicating that they came from members of a single clone. The last species, *H. tuberosus*, (Fig. 4) has a wide distribution in central and eastern North America, broadly overlapping the areas of the previous two species, and extending into the range of *H. subrhomboideus* in the north central states. In general, it grows in somewhat wetter habitats than do the others. As the "Jerusalem artichoke," it has been widely cultivated and since it also readily escapes, it is practically impossible to determine its prehuman distribution. All of these species reproduce vegetatively from rhizomes or tubers and are quite aggressive, frequently bcoming established as escapes.

MORPHOLOGY: In their extreme forms, the four taxa considered here are quite distinct, but intergradations are frequent in nature. The principal features of each are given in Table I. Many characters, such as leaves, are extremely variable and, hence, it is difficult to give precise measurements. The phyllaries (Fig. 5) seem to offer the most stable

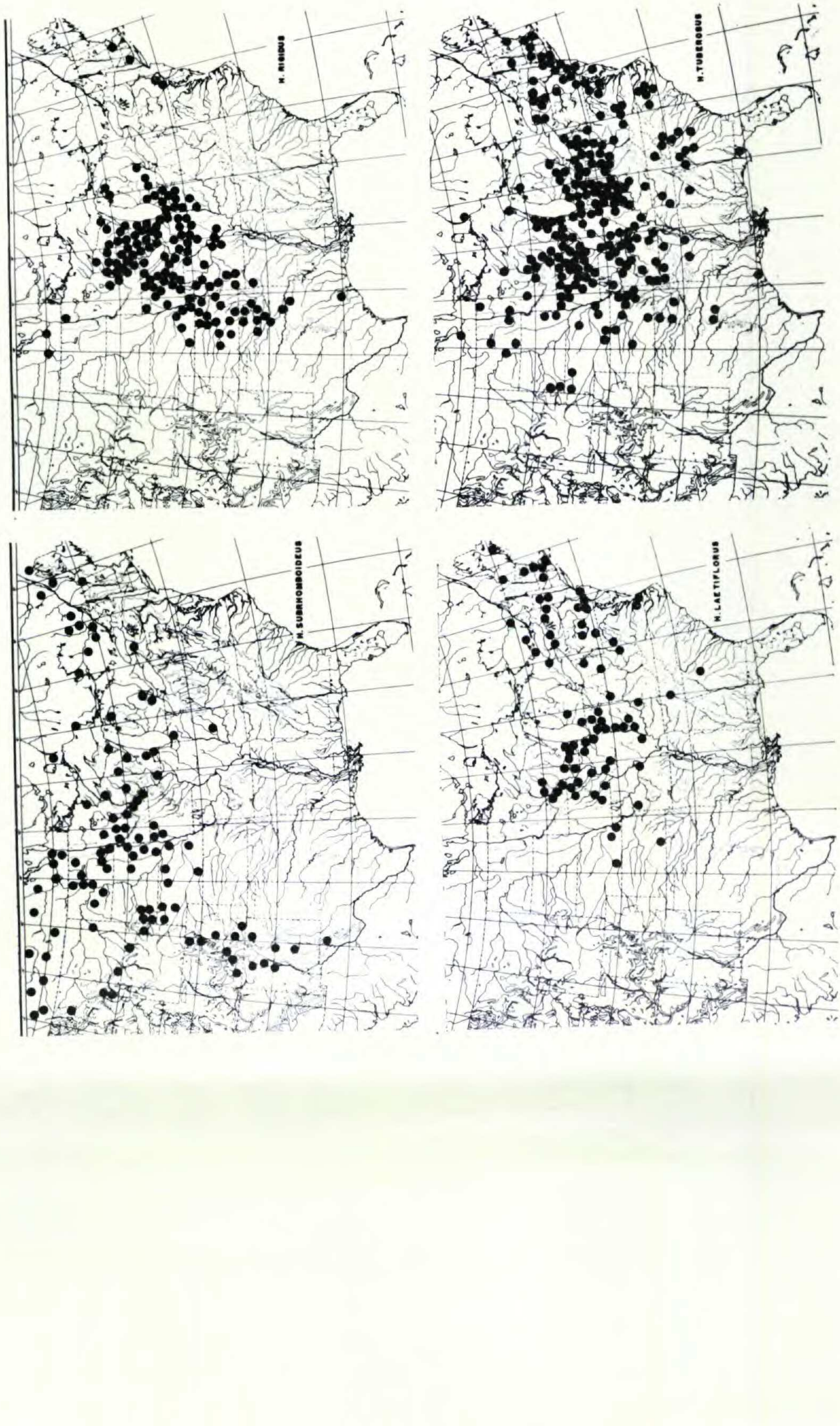

Figure 1-4. Maps showing the distribution of *H. subrhomboideus*, *H. rigidus*, *H. laetiflorus* and *H. tuberosus*. Base map used through the courtesy of Dr. R. E. Woodson, Jr. and the Missouri Botanical Garden.

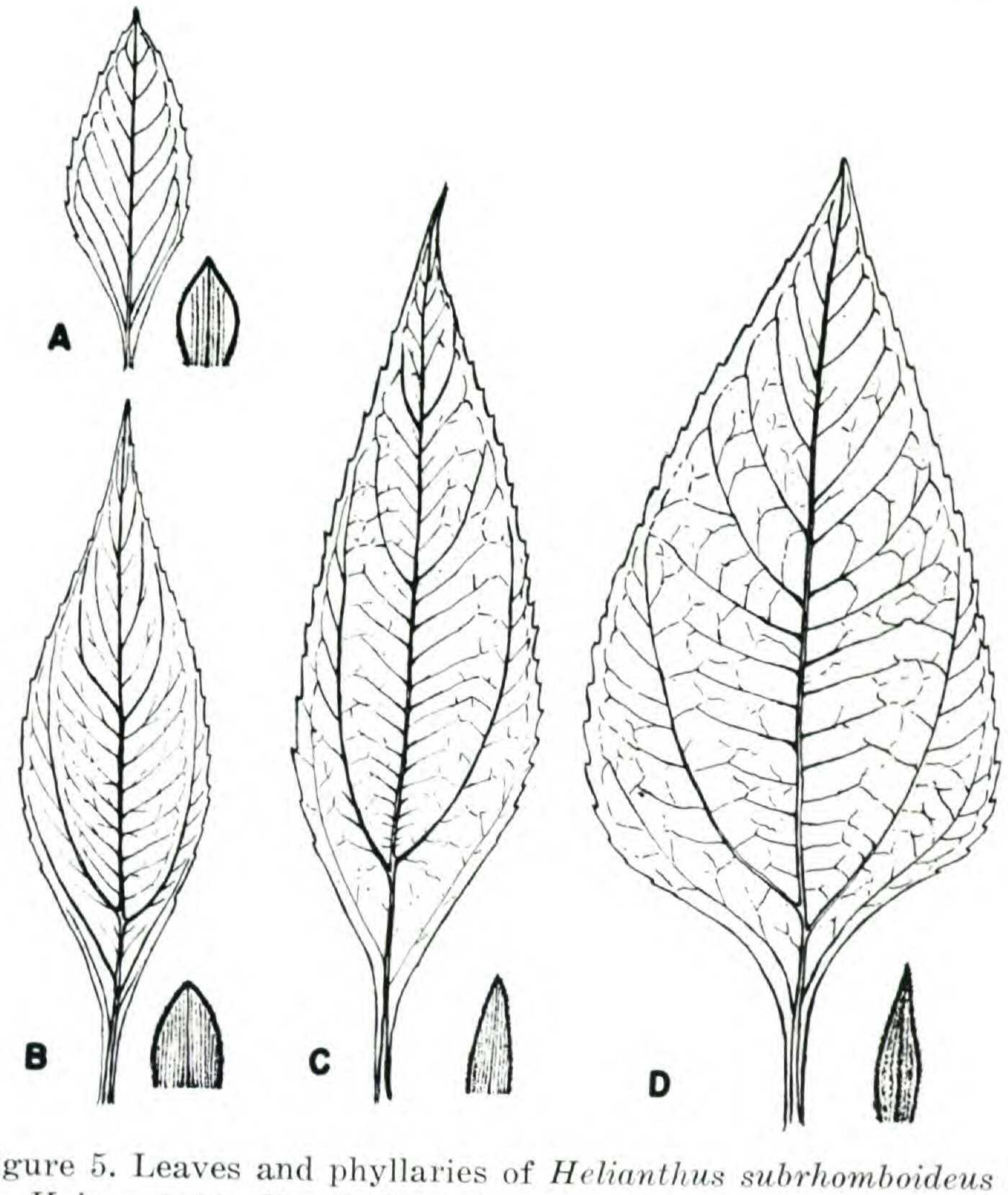

Figure 5. Leaves and phyllaries of *Helianthus subrhomboideus* (A) from *Heiser 3111; H. rigidus* (B), *Steyermark 9064; H. laetiflorus* (C), *Breitung 6154;* and H. tuberosus (D), *Ownbey 1166.* Leaves, × 2/5. Phyllaries, slightly enlarged.

characters, and perhaps are of the greatest value in delimiting the taxa.

From the table it can be seen that *H. subrhomboideus* and *H. tuberosus* represent the extremes. *Helianthus laetiflorus* has no unique features and is largely intermediate between *H. rigidus* and *H. tuberosus*. *Helianthus rigidus*, on the other hand, approaches either *H. subrhomboideus* or *H. laetiflorus* or is intermediate between them. A scatter diagram (Fig. 6), based on herbarium material, illustrates this situation for phyllary length and leaf length.

Artificial Hybrids: Reciprocal hybrids, excepting the

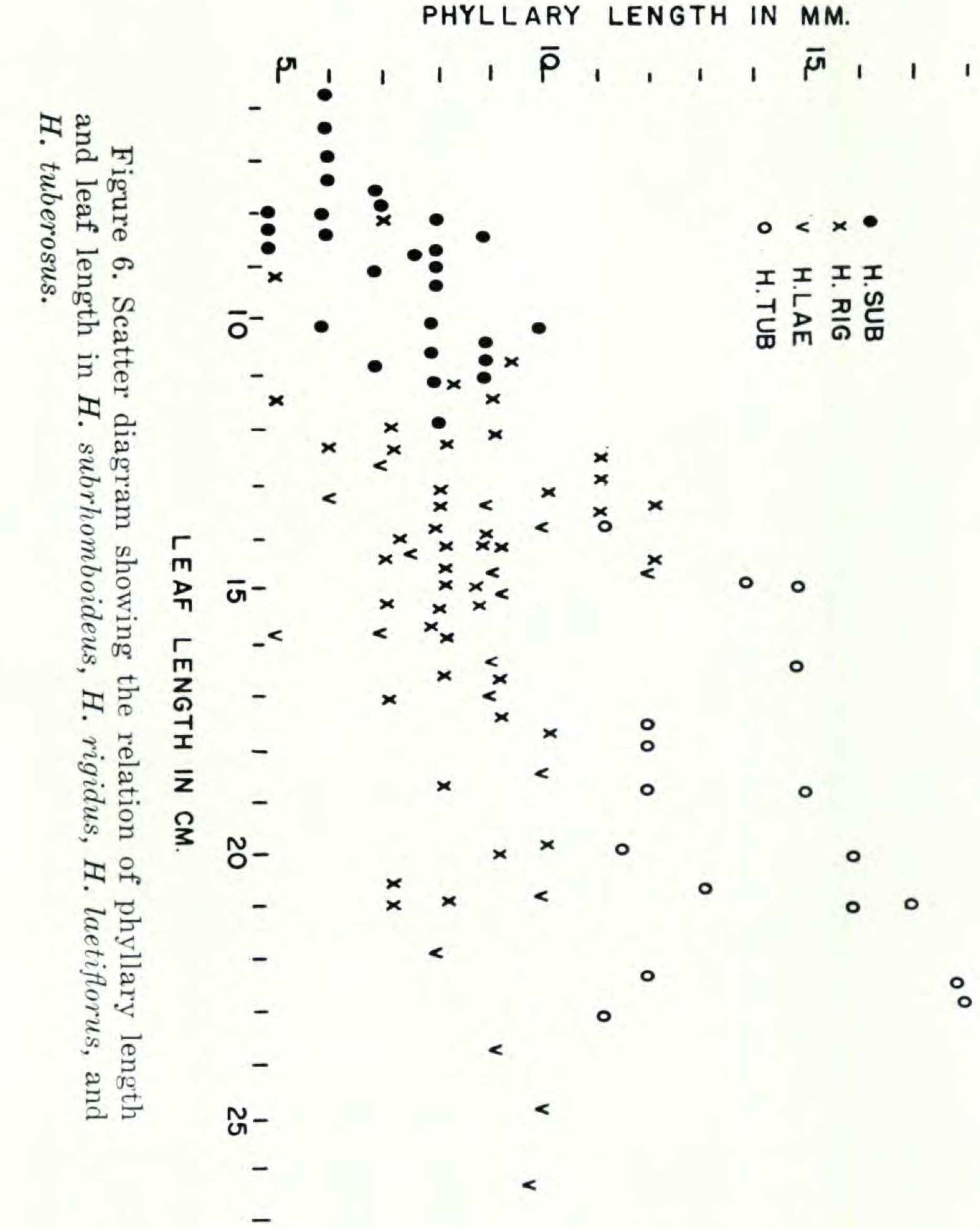

Figure 6. Scatter diagram showing the relation of phyllary length and leaf length in *H. subrhomboideus*, *H. rigidus*, *H. laetiflorus*, and *H. tuberosus*.

combination, *H. subrhomboideus* × *H. laetiflorus*, have been made involving the four taxa discussed above. All of the hybrids obtained were vigorous and fertile and largely intermediate morphologically with the exception of those so indicated below. Hybrids have also been made between sister plants and between different races of *H. subrhomboideus* and *H. tuberosus*, and all gave progeny closely resembling their parents. Since all of these species are normally self-incompatible, it has been impossible to obtain

TABLE 1

COMPARISON OF CERTAIN MORPHOLOGICAL FEATURES OF FOUR HEXAPLOID SUNFLOWERS

	H. subrhomboideus	*H. rigidus*	*H. laetiflorus*	*H. tuberosus*
Tuber	lacking	lacking	occasionally present	frequently present
Stem	usually simple	simple to branched	branched	branched
height	0.5-1.0 m.	0.8-2.0 m.	1.5-2.5 m.	1.8-2.6 m.
Leaves	opposite	opposite to alternate	upper alternate	upper alternate
surface	scabrous below	scabrous below	scabrous below	glabrous to puberulent or tomentulose below
length	5-12 cm.	8-27 cm.	12-25 cm.	14-23 cm.
color	grey-green to light-green	grey-green to light-green	grey-green to dark-green	dark-green
shape	linear to rhombic or ovate	lanceolate to ovate	lance-ovate	lance-ovate to ovate
petiole	very short	short to medium	medium	long
Peduncles	long, leafless	long, nearly leafless	medium long with reduced leaves	short, leafy
Disk-flowers	dark, red-brown	red, rarely predominately yellow	yellow or only slightly red	yellow
Phyllaries	tightly appressed	tightly appressed	appressed	loose, sometimes reflexed
shape	elliptical to oblong-ovate	oblong-ovate	oblong-lanceolate	lanceolate
pubescence				
margin	conspicuously ciliate	conspicuously ciliate	conspicuously ciliate	inconspicuously ciliate
surface	glabrous	glabrous	glabrous to pubescent	frequently pubescent
length	shorter than disk 5-10 mm.	shorter than disk, 5-12 mm.	equalling the disk, 5-12 mm.	longer than disk, 11-18 mm.

selfs. The small population size of most of the hybrid populations resulted from failures of seed germination which is not uncommon among perennial sunflowers. Herbarium specimens of the parents and representatives of the hybrid populations are deposited at Indiana University.

H. subrhomboideus × *H. tuberosus* (P29 x P59). The 15

reciprocal F_1's were largely intermediate, but with a leaf shape nearer *H. subrhomboideus* and phyllaries with acute tips similar to that of *H. laetiflorus*. Seventeen F_2 plants were secured which showed a variety of leaf shapes approaching, but not reaching the parental types. All had phyllaries similar to *H. laetiflorus* and the amount of stainable pollen varied from 70 to 95%. Most of the F_2 plants would have been identified as *H. laetiflorus* had they been collected in the wild. Meiosis in the F_1 showed mostly pairs with a few multivalents, which is similar to the pairing found in the parental species. An F_1 generation between P29 x P21 gave plants essentially similar to the above. In an F_2 of 29 plants of this combination most of the plants were nearer to *H. rigidus*, although some broad leaf and yellow disk segregation appeared. Thirteen of these plants showed considerable weakness and died before maturity.

H. subrhomboideus × *H. rigidus* (P79 x P147A). The seven F_1's were for the most part intermediate in morphology and fertile.

H. rigidus × *H. tuberosus* (P147A x P21). The three F_1 plants obtained were intermediate except for the leaves which were nearer to those of *H. tuberosus*. These plants were all fairly good matches for *H. laetiflorus*. An F_2 of 24 plants was grown and these were similar to the F_1 plants or closely approached *H. tuberosus* in appearance.

H. rigidus × *H. laetiflorus* (P147A x N3). The F_1 generation of twenty plants was fairly uniform, and the plants resembled typical *H. rigidus* except for the more leafy peduncles and variations in leaf shape and size.

H. rigidus × *H. laetiflorus* (P147A x B). Seeds for both of the parent plants came from the same population in White County, Illinois. Only three F_1 plants were obtained. Two of these were very similar to P147A, but the third had yellow disks and leaves resembling those of *H. tuberosus* in shape. In a second cross (P147 x Ar1) all of the 14 plants secured were more like the *H. rigidus* parent but one plant was completely sterile, two showed low pollen stainability (45 and 59%), and three were quite weak. A third combination (N3 x 147A) gave 11 plants which while showing

some plant to plant variation were essentially similar to *H. rigidus* and were all fertile.

H. laetiflorus × *H. laetiflorus* (P147B1 x 2). Although this cross was made several times, only one seed was ever obtained. The plant secured from it was nearly sterile and had leaves resembling *H. tuberosus*, but with shorter petioles and a dense pubescence quite unlike that found in any of the species under consideration here. It is unlikely that contamination could have occurred, and moreover it is difficult to visualize any species that could have crossed with *H. laetiflorus* to produce such a hybrid. It is possible that the plant represents a type of recombinant which is not successful in the wild. More than 50 seeds were obtained in a cross involving two different accessions of *H. laetiflorus* (N3 x Ar1) but only one seed germinated giving rise to a fertile plant, approaching *H. rigidus* in appearance.

H. laetiflorus × *H. tuberosus* (P147B x P22). Thirty-seven F_1's, were secured, all of which appeared very similar to the *H. tuberosus* parent except for the slightly shorter phyllaries. Some of the plants showed reduction in seed set when intercrossed or backcrossed, but when open pollinated gave good seed set. Fifty F_2 plants were grown which gave segregates approaching the parental types as well as the plants similar to the F_1. A second cross of these two species (H408 x Ar1) gave only five seeds, one of which germinated to give rise to a plant with 93% pollen stainability and showing some features of both parents.

These crosses indicate that hybrids involving these four taxa are readily obtained, and that with the exception of certain crosses involving *H. laetiflorus* are fertile and vigorous. Moreover, it is clear that hybrids between either *H. subrhomboideus* or *H. rigidus* with *H. tuberosus* give plants resembling *H. laetiflorus*. It is unfortunate that more hybrids of *H. laetiflorus* × *H. laetiflorus* were not secured, but it does appear significant that neither of the two plants obtained from this cross resembled their parent.

PROGENY TESTS: P68. *H. laetiflorus*. Three plants were secured which showed considerable variation, particularly in regard to leaf shape and size. Plants of *H. tuberosus* are

known to occur in the area and could have served as the pollen parent.

L1. The parent plant was somewhat intermediate between *H. tuberosus* and *H. laetiflorus*. One of the three offspring resembled *H. rigidus* and the other two approached *H. tuberosus*.

L2. *H. laetiflorus*. The 11 offspring produced little pollen but the stainability ranged from 60 to 90% with a mean of 79%. The plants all showed various combinations of characters of *H. laetiflorus* and *H. tuberosus*.

Although the pollen parent is unknown for all of these plants, they are of significance in showing either that natural cross pollination takes place between species or that *H. laetiflorus* shows segregation.

DISCUSSION: Although the four hexaploid sunflowers, *H. subrhomboideus*, *H. rigidus*, *H. laetiflorus*, and *H. tuberosus*, are quite distinct in their extreme form, they intergrade so freely that it is difficult to describe limits to these taxa. This blurring of the species boundaries could be explained by natural hybridization, and it is possible that two of the taxa, *H. laetiflorus* and *H. rigidus*, are of hybrid origin.

Plants which have been identified as *H. laetiflorus* could represent F_1 hybrids or hybrid derivatives of *H. tuberosus* × *H. rigidus* (or perhaps *H. subrhomboideus*). The evidence for this conclusion rests on the following: (a) *H. laetiflorus* has no unique characters, but combines various features of its putative parents; (b) artificial hybrids between the postulated parents can be obtained and would be classed as *H. laetiflorus;* (c) *H. laetiflorus* apparently does not breed true from seed; and (4) this taxon is generally found in areas where the two supposed parents grow. The species was described in 1807 from plants grown in Europe, and although only one of its putative parents was known there at this time, we nevertheless feel that it is most likely that the type is based on a hybrid (Heiser, 1960).

Helianthus rigidus might be postulated to have a hybrid origin from *H. subrhomboideus* × *H. tuberosus*. *Helianthus rigidus* shows no character which could not have come from

the supposed parents, although it does occur in areas outside of the range of one of the "parents" (Fig. 2). If it were to have originated from introgression of *H. tuberosus* into *H. subrhomboideus*, however, selection for certain introgressive types might have resulted in constancy and the introgressants might have been able to invade new areas or effectively replace *H. subrhomboideus*.

Since the species are all polyploids, certain other explanations for the intergradation must be explored. Although at present we cannot definitely identify all the diploid progenitors, it is likely that the hexaploids are partly or entirely allopolyploid in origin. Kostoff (1939) on the basis of analysis of the hybrid between *H. annuus* and *H. tuberosus* has suggested the genomic formula $A_{t1}A_{t1}A_{t2}A_{t2}B_tB_t$ for *H. tuberosus* with the B genome being nearly homologous with that of *H. annuus*. The A_t genomes could come from one of the three closely related tetraploids of the eastern United States, *H. hirsutus*, *H. strumosus*, or *H. decapetalus* which themselves may be of alloploid origin (Smith, 1961). Most hybrids of the diploid perennials exhibit good pairing (Heiser, *et al.*, 1962) which could account for the similarity of the two A genomes postulated by Kostoff for *H. tuberosus*. Let us therefore, for the present study, assume a genomic formula for *H. tuberosus* of $A_1A_1A_2A_2BB$. *Helianthus laetiflorus* might conceivably be $A_2A_2A_3A_3BB$; *H. rigidus*, $A_3A_3A_4A_4BB$; and *H. subrhomboideus* $A_4A_4A_5A_5BB$, where A_1, A_2, etc. represent genomes from closely related perennial diploids. Such a hypothesis would explain the essentially good pairing and interfertility between all the hexaploid species as well as the morphological similarities and differences.

Segregation in such polyploids might give results resembling interspecific hybridization. Stebbins (1950) has pointed out that segmental allopolyploids, in contrast to strict alloploids, may give segregates approaching one or the other of the parents. Smith (1961) found plants of the tetraploid *H. strumosus* apparently showing introgression from *H. hirsutus*, even though the latter did not grow in

the same area, and he suggested the possibility of allotetraploid segregation. Although we have no evidence that allopolyploid segregation is occurring in the hexaploids, it nevertheless offers an alternative hypothesis to interspecific hybridization.

It is, of course, feasible that we may have various combinations of the possibilities discussed above — part of the variability may result from allopolyploid segregation, part from hybridization. Considering all the possibilities, however, we feel that there is fairly good evidence that *H. laetiflorus* is a hybrid. On the other hand, while *H. rigidus* may owe its origin to hybridization, we do not feel that any definite decision can be reached at present.

In regard to taxonomic treatment, this group of taxa offers certain difficulties inherent in many plants of polyploid origin which have no barriers to interbreeding. *Helianthus tuberosus*, in spite of some intergradation with other species, deserves recognition as a species. On the other hand, if *H. laetiflorus* is a collection of hybrids or hybrid derivatives, it does not deserve designation as a species. Although in general, we are opposed to giving distinct names to hybrids, in the case of a well established binomial, it is perhaps best to continue its use with indication that it is a hybrid.[1] The authors are not in agreement as to the treatment of the other two taxa. One feels that *H. subrhomboideus* should be treated as a species and *H. rigidus* as a hybrid, whereas the other thinks that they should be considered races of a single species. If the latter course is adopted, *H. subrhomboideus* becomes a subspecies of *H. rigidus*.

SUMMARY: The four hexaploid sunflowers, *H. subrhomboideus*, *H. rigidus*, *H. laetiflorus*, and *H. tuberosus* form a morphological series with the first and last named species representing the extremes. Artificial hybrid combinations of all the species, except *H. subrhomboideus* × *H. laetiflorus*, were largely fertile. Certain of the hybrids of *H. tuberosus* × *H. subrhomboideus* and *H. rigidus* strongly resemble *H.*

[1]The name then becomes *H.* x *laetiflorus* Pers. (pro. sp.) Syn. 2: 476. 1807.

TABLE II

SOURCE OF PLANTS USED IN THE CROSSES AND PROGENY TESTS

Number	*Name*	*Locality and Collector*
Ar1	*H. laetiflorus*	Cult. Monroe Co., Ind. (Heiser)
H408	*H. tuberosus*	Darke Co., Ohio (R. T. Neher)
L1	*H. laetiflorus-tuberosus*	Auburn, Mass. (B. N. Gates)
L2	*H. laetiflorus*	Worcester, Mass. (B. N. Gates)
N3	*H. laetiflorus*	White County, Ind. (Heiser)
P21	*H. tuberosus*	Polk Co., Iowa (Heiser)
P29	*H. subrhomboideus*	Cass Co., N. D. (O. A. Stevens)
P59	*H. tuberosus*	Hennepin Co., Minn. (Gerald Ownbey)
P68	*H. laetiflorus*	Cult. Monroe Co., Ind. (Heiser)
P79	*H. subrhomboideus*	Lawrence Co., Ind. (Heiser)[2]
P147A	*H. rigidus*	White Co., Ill. (Heiser)
P147B	*H. laetiflorus*	White Co., Ill. (Heiser)

laetiflorus. On the basis of the study of morphology, geographical distribution, and the hybrids, it is suggested that *H. laetiflorus* is of hybrid origin and that *H. rigidus* possibly represents an introgressant. On the other hand, it is also possible that allopolyploid segregation is occurring in these species giving results suggestive of hybridization.

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[2]Plants from this same colony *(Kriebel 3965)* were originally identified as *H. silphioides* Nutt. by Fernald (1946) who later admitted his misidentification in a letter to the junior author. So far as is known *H. silphioides* does not occur in Indiana.

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